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Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season and fish length

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Abstract – We quantified microhabitat use by members of a southern Appalachian stream fish assemblage over a ten-year period that included both floods and droughts. Our study site (37 m in length) encompassed riffle, run and pool habitats. Previous research indicated that species belonged to either benthic or water-column microhabitat guilds. Most species exhibited non-random microhabitat use in all seasons, and benthic and water column species generally were over-represented in the deeper portions of the site. In addition, water column species generally were over-represented in microhabitats with lower average velocities. The majority of seasonal shifts in microhabitat use were passive (i.e. correlated with changes in microhabitat availability), whereas, most shifts associated with hydrological periods appeared to be active responses to changing environmental conditions. Most species exhibited length-related shifts in microhabitat use, which were strongly affected by hydrologic period for four of ten species. Microhabitat use patterns of assemblage members appeared to be a consequence of species-specific responses to changing environmental conditions. The highly flexible patterns of microhabitat use exhibited by these species necessitate that decisions regarding their management be based on data covering a range of environmental conditions.

Key words: assemblage structure; spatial resource use; hydrologic variability; drought; stream fishes; coexistence

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Most fish have complex life histories that require that an individual pass through multiple developmental stages before reaching maturity (Moyle & Cech 1988). The ecological requirements of these stages may vary tremendously, as individuals typically progress from low-motility larva to free-swimming young-of-the-year, and finally enter the adult life history stage. It is possible that the high level of ecological flexibility required by complex ontogenies also has contributed to the ability of many adult fishes to utilize a wide range of ecological resources. For example, not only do many temperate fresh-water fish species (e.g. most members of the Salmonidae, Cyprinidae, Centrarchidae, Percidae) occupy multiple habitat types such as streams and lakes (Moyle & Cech 1988, Wooton 1992); even within a given habitat type, individuals sometimes shift their use of spatial and trophic resources in response to seasonal, annual, and disturbance-related changes in resource availability (Angermeier 1987, Moyle & Cech 1988, Grossman & Sostoa 1994a, b, Wood & Bain 1995).

The substantial variation in resource use exhibited by many fishes presents a special challenge for researchers in both fish ecology and fisheries management. For example, given that fishes commonly occupy both multiple habitat types and trophic levels during their life span, rigorous tests of resource-based ecological models (e.g. limiting similarity, optimal foraging, food web regulation) will require: 1) resource use data for multiple life history stages of the species being examined, and 2) quantification of how variations in resource availability affect resource use (Werner & Gilliam 1984). Similar data requirements also affect our ability to develop, test, and utilize models for the conservation and management of fish populations. For example, resource use-based management models such as the Instream Flow Incremental Methodology (Bovee 1982), Habitat Suitability Index (Pajak & Neves 1987), and Index of Biotic Integrity (Fausch et al. 1990) require characterization of the ecological requirements of fish species or assemblages over the range of environmental conditions that they are likely to experience during their life span (Orth 1987). Curiously, despite the importance of resource use data to both fish ecologists and fisheries managers, there are almost no long-term (i.e. ≥5 years) studies of resource use within fish assemblages (but see Ross et al. 1987). In fact, it is possible that the lack of such data has limited the ability of fish ecologists and fisheries managers to predict the effects of environmental change (e.g. climatic cycles) or perturbations (e.g. impoundments, acid precipitation) on fish assemblages.

Given the paucity of long-term studies of resource use by fish, we decided to quantify the use of spatial resources over a ten year-period within an assemblage of stream fishes occupying Coweeta Creek, North Carolina, USA. Most temperate streams exhibit substantial environmental variation, which makes accurate quantification of the inhabitant's ecological requirements particularly important for tests of theory or scientific management. In fact, environmental variation in Coweeta Creek was substantial during our study, and this drainage experienced near record values for both high and low annualized mean daily flows over the course of our research (Grossman et al. 1995a). Hence, these data should yield useful information on how extensive fluctuations in flow rates and water levels affect microhabitat use by assemblage members.

The Coweeta Creek fish assemblage is dominated by species that are broadly distributed across North America, i.e., mottled sculpin (*Cottus bairdi*), longnose dace (*Rhinichthys cataractae*), stoneroller (*Campostoma anomalum*), greenside darter (*Etheostoma blennioides*), northern hogsucker (*Hypentelium nigricans*), creek chub (*Semotilus atromaculatus*), rock bass (*Ambloplites rupestris*) and rainbow trout (*Oncorhynchus mykiss*) (Lee et al. 1980, Grossman et al. in press). This assemblage also contains several species whose distributions are more restricted (e.g. rosyside dace – *Clinostomus funduloides*, river chub – *Nocomis micropogon*, and warpaint shiner – *Luxilus coccogenis* (Lee et al. 1980). Hence, this database should be of use to researchers and managers working on both regional and broader geographic scales. The specific questions we addressed were as follows. First, do species exhibit stable long-term patterns of non-random microhabitat use or does environmental variation in the form of seasonal or hydrologically related changes in microhabitat availability have a strong impact on these patterns? Second, what effect does environmental variation have on length-related patterns of microhabitat use?

Methods

This study augments earlier work by Grossman & Freeman (1987), which presented data from the first two years (1983–1984) of this study, and complements a companion paper which focuses on how environmental variation affects assemblage structure, and potential competitive and predatory interactions among these fishes (Grossman et al. in press). Hence, many of our methods have been described elsewhere and will be reiterated only briefly.

The study site

We observed fishes in a 37-m section of Coweeta Creek. This site encompassed the home ranges of

Table 1. Classification of microhabitat use samples with respect to season and hydrologic period (after Grossman et al. in press). Hydrologic periods are as follows: PR=pre-drought, D=drought, PO=post-drought.

Spring collection	Summer collection	Autumn collection
22 March–24 April 1984 (PR)	11 July–10 Aug. 1983 (PR)	26 Oct.–9 Nov. 1983 (PR)
28 April–27 May 1988 (D)	5 July–18 Aug. 1984 (PR)	26 Sept.–11 Nov. 1984 (PR)
26 April–11 May 1990 (PO)	20 Aug.–5 Sept. 1986 (D)	9 Nov.–19 Nov. 1986 (D)
	5 Aug.–18 Aug. 1988 (D)	13 Oct.–19 Oct. 1989 (PO)
	8 Aug.–10 Aug. 1989 (PO)	16 Oct.–1 Nov. 1990 (PO)
	4 Aug.–19 Aug. 1990 (PO)	27 Oct. 1992 (PO)
	26 Aug.–1 Sept. 1992 (PO)	

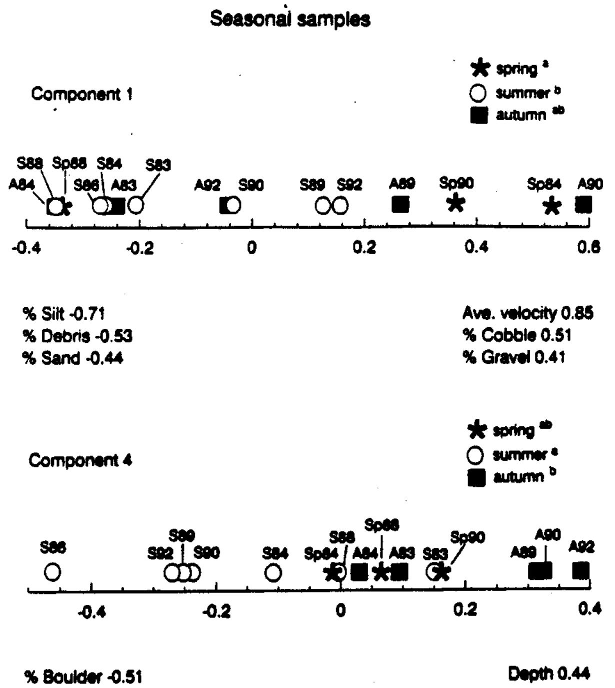

Fig. 1. Principle components that exhibited significant seasonal differences in microhabitat availability analysis. We have only presented variables with loadings >|0.40| on a given component. Sample abbreviations indicate the season (i.e., Sp=spring, S=summer, and A=autumn) followed by the last two digits of the year. Seasonal means with the same letter did not differ significantly using Kruskal-Wallis tests coupled with Tukey-Kramer a posteriori tests on mean component scores. These data are after Grossman et al. (in press).

many of the resident species in this assemblage (Hill & Grossman 1987, Freeman et al. 1988). The site was located in a fifth order section of Coweeta Creek and consisted of riffle-run-pool habitat. Streams with visually similar physico-chemical and biological characteristics are found throughout the southern Appalachian region.

Microhabitat availability

We defined and quantified microhabitat availability using the methods of Grossman & Freeman (1987) and the sampling regime (Table 1) of Grossman et al. (in press). In brief, availability data were collected by measuring depth (by straightedge, nearest cm), average velocity (electronic velocity meter±0.1 cm/s, criteria of Bovee & Milhous 1978), and the percentage contribution (visual estimate) of the following materials (bedrock, boulder, cobble, gravel, sand, silt, and debris) to the substratum in randomly located 20×20 cm quadrats (Grossman & Freeman 1987). Between 30 and 50 quadrats were examined per sample (see Grossman & Freeman 1987). We categorized substrata other than debris on the basis of maximum particle dimensions (bedrock [embedded to the surface] & boulders [unembedded particles] >30 cm, cobble ≤30 and >2.5 cm, gravel ≤2.5 cm and >0.2 cm, sand ≤0.2 cm, and silt – material that was capable of suspension in the water column, Grossman & Freeman 1987). Debris was not separated into size classes (Grossman & Freeman 1987). We collected microhabitat availability data either during, or just after, a several day to several week period of fish microhabitat use observations. Microhabitat availability and fish microhabitat use measurements always were made on separate days. Microhabitat availability data for the autumn 1986 sample were strongly affected by a storm, hence, these data were not used for analyses of: 1) non-random microhabitat use, and 2) seasonal or hydrologically related shifts in microhabitat use. Water temperature data indicate that the drought only produced slight, albeit inconsistent, increases in this parameter in the site (Grossman et al. in press), and as a consequence, will not be redescribed.

Between 1985 and 1988, the southeastern United States experienced a severe drought, which resulted in low mean daily flows in Coweeta Creek (Grossman et al. 1995a). Consequently, we also classified samples on the basis of their temporal relationship to the drought [i.e. pre-drought, drought, or post-drought, Table 1].

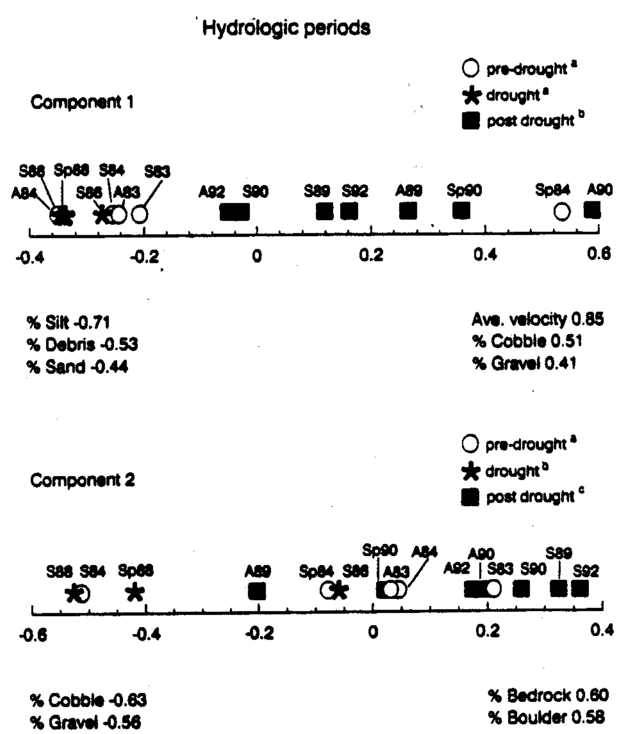

Fig. 2. Principle component analyses for microhabitat availability data from different hydrologic periods. See Fig. 1 for further information. These data are after Grossman et al. (in press).

Mean annaualized daily flows for these three periods averaged: 1) pre-drought – $0.33m^3/s$, 2) drought – $0.17m^3/s$, and 3) post-drought – $0.35m^3/s$ (Grossman et al. 1985). We tested for significant differences in microhabitat availability by classifying samples on the basis of either season or hydrologic period (i.e. pre-drought, drought or post-drought), and then subjected them to the principle component method of Grossman & Freeman (1987) (see statistical analysis – seasonal differences in microhabitat use). Substratum estimates that differed by less than 2% were considered within the range of observer error and hence equal. Although we have tried to minimize redundancies, microhabitat availability data also were required, and hence presented, for the analysis of Grossman et al. (in press).

Fish microhabitat use

We conducted fish observations by entering the site from its downstream border and snorkeling in an upstream direction. We then recording the positions of undisturbed specimens and obtained the following measurements: focal point velocity (i.e. at the fishes' position, electronic velocity meter$\pm$0.1 cm/s), distance from substratum (straightedge, nearest cm), distance from shelter (straightedge, nearest cm), average velocity (electronic velocity meter$\pm$0.1 cm/s, criteria of Bovee & Milhous 1978), depth (straightedge, nearest cm), and substratum composition (see microhabitat availability). Shelter was defined as any object capable of concealing at least 50% of the fish's body. All techniques are described in detail in Grossman & Freeman (1987) and Grossman et al. (in press). Our observations were restricted to day light hours because these fishes appeared to be relatively quiescent, or occurred in similar microhabitats, at night in Coweeta Creek (J. Hill, J. Barrett, A. Thompson, and G. Grossman, personal observations). Similar techniques have been used to quantify microhabitat use by stream fishes in both Europe and the United States (Baltz & Moyle 1985; Grossman & Freeman 1987; Greenberg 1991; Grossman & De Sostoa 1994a, b). Previous work indicated that species could be classified as members of either benthic or water column microhabitat guilds (Grossman & Freeman 1987; Grossman et al. in press) and we have followed that convention here (benthic guild: *Ca. anomalum*, *Co. bairdi*, *E. blennioides*, *H. nigricans*, *R. cataractae*; water column guilds: *A. rupestris*, *Cl. funduloides*, *L. coccogenis*, *N. micropogon*, *O. mykiss*, *S. atromaculatus*). In Grossman & Freeman (1987) *Ca. anomalum* was misidentified as *Ca. oligolepis*.

Statistical analysis

We quantified non-random microhabitat use using the methods of Grossman & Freeman (1987). First we subjected the microhabitat availability data for a given season to a principle component analysis using the correlation matrix. We only interpreted components that had eigenvalues >1.0 and elucidated ecologically meaningful patterns of variation. The microhabitat use data for each species (minimum $n=5$) were then multiplied by the scoring coefficient matrix of the availability data principle component analysis. This yielded a score for all components for each specimen, and these data were summed to provide score distributions for each species on each component. We then compared the score distributions for each species to those of the availability data, using a chi-square statistic ($P=0.05$). If a significant result was obtained, we partitioned the analysis to identify the significant classes within the distribution (Zar 1984). In all cases where data were tested repeatedly, the Dunn-Sidak procedure (Ury 1976) was used to control alpha at 0.05. These techniques enabled us to depict microhabitat use by fishes within a multidimensional habitat gradient scaled by availability. In addition, the partitioned chi-square analysis allowed us to specifically identify the subset of the gradient upon which species were over- or under-represented. These methods have proved useful in elucidating non-random microhabitat use in both descriptive and experimental studies of stream fishes (Grossman & Freeman 1987, Freeman et al. 1990, Grossman & Boule 1991, Grossman et al. 1995b).

We identified seasonal, hydrologic, and length-related differences in microhabitat use, by again subjecting fish microhabitat data to a principal component analysis. We used these data to test for significant differences in mean component scores with respect to the parameter of interest (i.e. season, hydrologic period or length class). Significant differences in principal component analysis scores were assessed using Kruskal-Wallis tests and Tukey-Kramer a posteriori tests. We also examined results for potential biases caused by covariation among parameters (e.g. were seasonal differences in microhabitat use affected by seasonal changes in mean fish length). Length classes were arbitrarily chosen to maximize the number of classes examined while ensuring that the number of specimens per length class was still sufficient for statistical testing (i.e. $n \geq 5$). For length-related analyses, we first tested for significant differences in mean fish length across seasonal samples and hydrologic periods. Because most species exhibited such differences, we conducted analyses on two data sets: one which included specimens from all samples pooled, and the second consisted of separate data sets for each seasonal sample. Two analyses were warranted because data from individual seasons frequently yielded non-significant results. Examination of these data, however, suggested that this was a consequence of the small sample sizes produced when data for a given species from a single seasonal sample were then separated into different size groups.

Results

Effects of seasonal and hydrologic variation on microhabitat availability

A majority (68%) of the variance in the microhabitat availability data set was explained by the significant components from the PCA. Three ecologically interpretable components were extracted from availability data, although only two of these exhibited significant differences among either seasonal or hydrologic periods (Fig. 1, 2). In seasonal analysis, component one indicated that spring samples had the highest water velocities, greatest quantities of cobble and gravel and lowest amounts of depositional substrata. In contrast, summer samples had the lowest water velocities, lowest amounts of gravel and cobble and greatest amounts of depositional substrata (Fig. 1). Autumn samples had intermediate characteristics and were not statistically distinguishable from either spring or summer samples. The results for component four demonstrated that summer samples had shallower depths with greater quantities of boulders than autumn samples. Our seasonal microhabitat availability analyses probably were influenced by unequal sampling effort (e.g. autumn data lacked drought samples).

Hydrologic analysis demonstrated that post-drought samples had the highest water velocities, greatest quantities of erosional substrata, and lowest amounts of depositional substrata (Fig. 2). In contrast, samples from the drought had the lowest water velocities, lowest amounts of erosional substrata and greatest quantities of depositional substrata. Samples from pre-drought were intermediate between post-drought and drought samples, although they did not differ from drought on component 1. The analysis of availability data by hydrologic period yielded a greater level of statistical separation among samples than seasonal analyses (Fig. 2), which suggests that the drought had a stronger effect on microhabitat availability than seasonal variation.

Non-random microhabitat use

The principal component analysis of microhabitat availability data from individual seasonal samples extracted significant components that explained between 75 and 80% of the variance present in the availability data sets. All principal component analysis from individual samples extracted between three and four significant components, although species generally did not display non-random microhabitat use on all components (Table 2). The primary microhabitat gradient elucidated by the principal component analysis (Table 2) separated high-velocity areas with a substratum dominated by erosional materials from low-velocity microhabitats with a substratum consisting mostly of depositional materials (Table 2). In four of ten samples, depth was positively correlated with water velocity, and regardless of velocity, depth generally was positively correlated with increasing quantities of erosional substrata and frequently correlated with decreasing quantities of depositional substrata (Table 2). These results indicate that the site contained elements of a riffle-run-pool continuum; however, the presence of deep high velocity areas dominated by erosional substrata suggests that such a characterization is overly simplistic for this site.

Most benthic species were over-represented in deeper areas of the site over erosional substrata (Table 2). Benthic guild members occasionally did not exhibit non-random use (Table 2) although this generally only involved either *Co. bairdi* (6 of 10 seasons) or *H. nigricans* (3 of 6 seasons) and did not appear to be related to sample size (Table 2). With respect to species-specific responses (in order of numerical abundance), *Co. bairdi* was found over a heterogeneous substratum whose composition changed seasonally (Table 2). *Rhinichthys cataractae* was over-represented in both deeper areas with erosional substrata as well as shallow locations with depositional substrata. This result was produced by the fact that seasonal samples contained varying numbers of large and small *R. cataractae*, which have distinct patterns of non-random microhabitat use (see length-related differences in microhabitat use). *Campostoma anomalum* typically occupied deep microhabitats with boulder or cobble substrata, although in some seasons (e.g. spring 1988, autum 1989) boulders also were avoided (Table 2). In the three seasons during which *H. nigricans* exhibited non-random use, it was over-represented in deep locations that typically possessed little bedrock or cobble and high amounts of boulder. In summer 1986, *E. blennioides* occupied deep microhabitats with bedrock substratum (Table 2).

Table 2. Means of microhabitat use data for PCA categories in which species were significantly over- or under-represented. Also presented are means and variable loadings (in parentheses) for microhabitat availability measurements. We only present data for variables with component loadings ≥|0.40|.

	n	Component	Score category range	Significant categories	No. exhibiting non-random use	Over (R)- or under (U)-represented	Average velocity (cm/s)	Depth (cm)	% bedrock	% boulder	% cobble	% gravel	% sand	% silt	% debris
Summer 1986															
Availability data	50						18	23	2	20	41	11	14	7	6
		1	−2.00 to 3.00				(−0.69)				(−0.62)	(−0.67)		(0.79)	(0.69)
		2	−3.00 to 1.50					(0.52)		(−0.91)		(0.47)	(0.54)		
		4	−3.50 to 2.50					(0.59)	(0.56)				(−0.51)		
Cl. funduloides	36	2	−1.00 to 2.00	0.50 to 2.00	32	R		43		1		15	32		
Co. bairdi	32						No significant categories								
E. blennioides	6	4	0.00 to 4.00	1.00 to 4.00	5	R		37	16				2		
N. micropogon	22						No significant categories								
O. mykiss	5						No significant categories								
R. cataractae	10	2	−1.50 to 0.50	−0.50 to 0.00	4	R		22		4		6	3		
S. atromaculatus	12	1	−1.50 to 3.50	1.00 to 3.50	6	R	1				7	1		47	19
		2	0.00 to 2.00	1.00 to 2.00	11	R		52		0		12	26		
Spring 1988															
Availability data	30						22	31	4	5	48	12	15	12	5
		1	−1.50 to 2.00				(−0.85)				(−0.64)		(0.81)	(0.82)	(0.44)
		2	−3.00 to 2.50					(0.65)		(−0.44)	(0.56)	(−0.55)			(0.48)
		4	−3.50 to 2.50						(−0.56)			(0.56)			(0.44)
Ca. anomalum	17	1	−1.00 to 0.50	−0.50 to 0.00	9	R	23				69		13	4	1
		2	−1.00 to 2.50	1.50 to 2.00	6	R		63		0	89	0			1
		4	−2.50 to 1.00	−2.50 to −1.50	7	R			5			1			1
Cl. funduloides	45	1	−1.00 to 2.50	−1.50 to −1.00	0[1]	U	45				71		3	1	3
		1	−1.00 to 2.50	−0.50 to 0.00	16	R	18				38		6	6	2
Co. bairdi	27						No significant categories								
L. coccogenis	24	1	−1.50 to 1.00	−0.50 to 0.00	11	R	18				54		8	5	2
N. micropogon	25						No significant categories								
O. mykiss	20	1	−1.50 to 2.00	−0.50 to 0.00	7	R	10				51		13	4	1
R. cataractae	9						No significant categories								
Summer 1988															
Availability data	30						12	20	8	3	53	15	8	11	2
		1	−2.00 to 2.00				(−0.68)					(−0.68)	(0.40)	(0.80)	(0.67)
		3	−2.00 to 3.00				(0.40)	(0.52)		(0.67)			(−0.58)		
		4	−2.50 to 3.00							(0.53)				(−0.41)	(0.42)
Ca. anomalum	17	3	0.00 to 2.50	−0.50 to 0.00	0[1]	U	14	19		0			6		
		4	−0.50 to 3.50	1.50 to 3.50	7	R				28				3	4
Cl. funduloides	35	1	−1.00 to 3.00	−1.50 to −1.00	0[1]	U	19					48	2	0	0
		3	−1.50 to 2.50	−0.50 to 0.00	4	U	13	40		0			20		
		4	−2.00 to 2.50	0.00 to 0.50	2	U				0				1	0

Table 2. (continued)

	n	Component	Score category range	Significant categories	No. exhibiting non-random use	Over (R)- or under (U)-represented	Average velocity (cm/s)	Depth (cm)	% bedrock	% boulder	% cobble	% gravel	% sand	% silt	% debris
Co. bairdi	26	4	−0.50 to 3.00	0.50 to 1.00	10	R				0				7	4
H. nigricans	8	3	−1.00 to 3.00	1.00 to 3.00	4	R	10	75		32			7		
		4	0.00 to 3.50	1.00 to 3.50	5	R				22				4	4
L. coccogenis	16	1	−0.50 to 2.50	0.50 to 1.00	7	R	6					19	33	5	4
		4	0.00 to 4.00	0.50 to 4.00	14	R				9				5	2
N. micropogon	25	1	−0.50 to 2.50	−1.50 to −1.00	0[1]	U	19					48	2	0	0
		3	−1.00 to 3.50	−0.50 to 0.00	0[1]	U	14	19		0			6		
		4	−0.50 to 4.00	−1.00 to −0.50	0[1]	U				0				10	0
		4	−0.50 to 4.00	0.00 to 0.50	1	U				0				4	0
O. mykiss	21	4	−1.00 to 2.00	1.50 to 2.00	6	R				2				5	7
R. cataractae	19	3	−1.50 to 3.00	1.00 to 3.00	8	R	22	35		31			6		
		4	−0.50 to 4.50	1.50 to 4.50	9	R				29				2	6
S. atromaculatus	22	1	−0.50 to 3.00	1.50 to 3.00	6	R	2					1	3	23	11
		3	−1.00 to 3.00	1.50 to 2.00	4	R	9	61		19			1		
Summer 1989															
Availability data	35						31	32	13	16	43	7	17	2	2
		1	−2.50 to 2.00				(0.49)	(0.61)	(0.54)	(0.49)	(−0.42)	(−0.46)	(−0.74)	(0.47)	
		2	−2.50 to 1.50				(0.71)		(−0.63)	(0.57)	(0.50)			(−0.65)	(−0.47)
		3	−2.00 to 3.00					(0.56)				(−0.68)	(0.43)		
		4	−3.00 to 2.00							(−0.54)	(0.72)				
Cl. funduloides	35	1	−0.50 to 2.00	−1.00 to −0.50	0[1]	U	11	27	4	0	53	2	35	0	
		3	−1.00 to 2.00	−1.50 to −1.00	0[1]	U		26				21	4		
Co. bairdi	19	1	−0.50 to 2.00	−0.50 to 0.00	8	R	16	40	0	5	48	11	22	8	
H. nigricans	5						No significant categories								
L. coccogenis	8	4	0.00 to 2.50	1.00 to 2.50	7	R				0	76				
N. micropogon	11	1	−0.50 to 1.00	0.00 to 0.50	7	R	23	79	2	9	65	4	15	3	
		2	−0.50 to 0.50	0.00 to 0.50	8	R	27		0	10	73			3	2
		4	−1.00 to 2.50	1.00 to 1.50	5	R				10	68				
O. mykiss	21	4	−2.00 to 2.50	1.50 to 2.50	8	R				0	88				
S. atromaculatus	11	1	−0.50 to 1.00	−0.50 to 0.00	5	R	8	60	0	0	32	3	31	16	
		2	−3.00 to 0.50	−3.00 to −1.50	7	R	2		0	8	16			19	18
		3	0.00 to 2.00	0.50 to 2.00	9	R		64				1	34		
Autumn 1989															
Availability data	34						35	30	6	6	55	12	10	3	8
		1	−2.50 to 1.50				(0.87)	(0.56)			(0.72)	(0.49)	(−0.53)	(−0.48)	(−0.56)
		2	−3.00 to 3.50					(0.41)		(−0.57)			(0.72)	(−0.51)	
		3	−2.00 to 2.00					(0.43)	(0.58)	(0.55)					(−0.43)
		4	−2.50 to 1.50						(−0.53)		(0.42)	(−0.66)			
A. rupestris	5	1	−2.50 to −0.50	−2.50 to −0.50	5	R	4	68			27	6	28	13	25
		2	0.00 to 1.50	0.50 to 1.50	4	R		68		0			25	14	

Table 2. (continued)

	n	Component	Score category range	Significant categories	No. exhibiting non-random use	Over (R)- or under (U)-represented	Average velocity (cm/s)	Depth (cm)	% bedrock	% boulder	% cobble	% gravel	% sand	% silt	% debris
Ca. anomalum	22	3	0.00 to 4.50	0.00 to 0.50	13	R		67	0	0					4
			0.00 to 4.50	1.50 to 4.50	6	R		67	9	79					0
		4	−1.00 to 2.50	1.50 to 2.50	14	R			4		82	0			
Cl. funduloides	31	1	−2.50 to 1.50	−1.50 to −0.50	19	R	11	53			34	3	21	11	5
		3	−0.50 to 4.50	−2.00 to −0.50	0[1]	U		21	0	1					11
		4	−3.00 to 2.00	−3.00 to 0.50	1	U			9		48	16			
Co. bairdi	22						No significant categories								
H. nigricans	7						No significant categories								
L. coccogenis	21	1	−2.00 to 1.00	−1.50 to −1.00	6	R	11	65			19	2	31	6	17
		3	−0.50 to 3.00	−1.00 to −0.50	0[1]	U		25	0	1					5
		4	−1.00 to 2.50	1.50 to 2.50	4	R			0		70	0			
N. micropogon	6	3	0.00 to 3.50	1.50 to 3.50	4	R		85	0	46					12
		4	0.50 to 2.00	1.00 to 2.00	5	R			0		35	3			
O. mykiss	27	3	0.00 to 5.00	−1.00 to 0.00	0[1]	U		30	0	1					7
		4	−3.00 to 3.00	2.00 to 3.00	5	R			0		87	0			
R. cataractae	12	1	−3.00 to 0.00	−3.00 to −0.50	11	R	6	17			25	6	27	31	9
S. atromaculatus	8	1	−2.50 to −0.50	−2.50 to −0.50	8	R	4	69			44	1	24	14	15
		3	−0.50 to 1.00	0.00 to 0.50	4	R		69	0	0					9
			0.50 to 2.00	1.00 to 2.00	7	R			0		46	1			
Spring 1990															
Availability date	35						34	35	6	15	55	11	4	7	3
		1	−4.00 to 1.50				(0.89)				(0.54)	(0.55)		(−0.86)	(−0.47)
		2	−2.00 to 2.50					(0.82)	(0.62)	(0.41)	(−0.63)				
		4	−2.50 to 2.50						(−0.61)				(0.67)		(0.50)
Ca. anomalum	8						No significant categories								
Cl. funduloides	37	1	−2.00 to 1.00	−1.00 to 0.00	27	R	14				51	3		8	6
		2	−2.00 to 3.00	−2.00 to −1.00	0[1]	U		16	0	1	76				
		4	−2.50 to 4.00	1.00 to 2.00	18	R			0				14		5
Co. bairdi	20						No significant categories								
H. nigricans	5	2	0.50 to 3.00	1.00 to 3.00	3	R		84	0	53	15				
		4	0.50 to 3.00	0.50 to 3.00	4	R			0				20		3
L. coccogenis	15	1	−1.50 to 1.50	0.50 to 1.50	0[1]	U	61				58	19		0	0
		2	−1.00 to 4.00	−1.00 to 0.00	0[1]	U		28	0	11	56				
N. micropogon	12	2	−0.50 to 3.00	0.50 to 1.00	5	R		76	0	5	60				
		4	0.00 to 3.50	1.50 to 3.50	5	R			0				16		20
O. mykiss	14	2	−0.50 to 3.50	0.50 to 1.00	6	R		86	0	5	72				
S. atromaculatus	7	2	0.00 to 1.50	0.50 to 1.00	3	R		65	0	0	44				
		4	1.00 to 3.50	1.50 to 3.50	6	R			0				21		17

Table 2. (continued)

	n	Component	Score category range	Significant categories	No. exhibiting non-random use	Over (R)- or under (U)-represented	Average velocity (cm/s)	Depth (cm)	% bedrock	% boulder	% cobble	% gravel	% sand	% silt	% debris
Summer 1990															
Availability data	35						20	33	15	15	40	8	16	5	1
		1	−2.50 to 2.00				(−0.59)		(−0.74)		(0.47)			(0.77)	(0.57)
		2	−3.00 to 2.00				(0.56)			(−0.41)	(0.43)	(0.56)	(−0.78)		
		3	−3.00 to 2.00					(0.84)			(0.64)	(−0.47)			
Cl. funduloides	30	2	−1.50 to 1.00	0.00 to 0.50	13	R	25			4	34	7	15		
		3	−1.00 to 2.00	−0.50 to 0.00	1	U		30			30	8			
Co. bairdi	21	1	−0.50 to 1.50	−2.50 to −1.00	0[1]	U	45		64		17			0	0
H. nigricans	6	1	−0.50 to 1.00	−0.50 to 0.00	5	R	17		3		33			5	0
		3	−0.50 to 1.50	0.50 to 1.50	5	R		78			40	11			
O. mykiss	13	1	−0.50 to 1.00	0.00 to 0.50	8	R	13		0		53			7	0
R. cataractae	9						No significant categories								
S. atromaculatus	11	1	−0.50 to 1.50	0.00 to 0.50	8	R	18		0		36			15	0
Autumn 1990															
Availability data	35						42	42	12	12	56	8	7	2	3
		1	−1.50 to 2.50				(−0.77)		(0.50)		(−0.63)		(0.58)	(0.57)	(0.46)
		2	−2.50 to 3.00					(0.40)	(−0.61)		(0.57)	(0.68)		(0.59)	
		3	−2.50 to 3.00							(0.55)	(−0.41)	(0.53)	(−0.40)		
		4	−2.50 to 2.00					(0.49)	(−0.57)	(0.46)					(0.48)
Ca. anomalum	10	4	0.50 to 3.50	1.00 to 3.50	7	R		81	0	47					9
Cl. funduloides	41	1	−1.00 to 3.50	−1.50 to −0.50	1	U	22		0		0		0	0	0
		4	0.00 to 3.50	−2.50 to 0.00	0[1]	U		24	21	0					1
Co. bairdi	22	1	−0.50 to 4.00	−1.00 to −0.50	0[1]	U	57		0		69		2	0	2
		2	−2.00 to 3.00	1.00 to 1.50	5	R		32	0		52	18		8	
		4	−2.50 to 3.50	2.00 to 3.50	3	R		33	0	0					41
H. nigricans	5						No significant categories								
L. coccogenis	17	1	−1.00 to 2.50	0.50 to 1.00	6	R	6		0		31		8	3	4
		3	−1.50 to 3.50	2.00 to 3.50	8	R				90	0	3	4		
		4	0.50 to 3.50	1.00 to 3.50	16	R		86	0	57					4
N. micropogon	6	3	−0.50 to 2.00	1.00 to 3.00	4	R				40	18	23	19		
		4	−0.50 to 2.50	1.00 to 2.50	5	R		78	0	32					1
O. mykiss	22	1	−1.00 to 2.00	−1.00 to −0.50	1	U	41		0		0		0	0	0
		4	−2.50 to 2.50	1.50 to 2.50	7	R		86	0	54					5
R. cataractae	12	1	0.00 to 4.00	1.50 to 4.00	8	R	3		0		18		23	31	22
		2	−2.00 to 2.00	1.00 to 1.50	5	R		33	0		35	5		24	
		4	−0.50 to 5.00	1.00 to 1.50	5	R		40	0	19					10

Table 2. (continued)

	n	Component	Score category range	Significant categories	No. exhibiting non-random use	Over (R)- or under (U)-represented	Average velocity (cm/s)	Depth (cm)	% bedrock	% boulder	% cobble	% gravel	% sand	% silt	% debris
Summer 1982															
Availability data	35						36	36	9	21	36	10	13	8	3
		1	−3.00 to 1.50				(0.87)	(0.72)		(0.52)				(−0.88)	(−0.55)
		2	−2.00 to 2.00						(−0.54)	(−0.43)	(0.80)	(0.82)			
		3	−2.00 to 2.50						(0.48)				(0.72)		
Cl. funduloides	33	1	−1.00 to 1.50	−3.00 to −1.50	0[1]	U	7	14		0				33	16
		3	−1.00 to 2.00	−2.00 to −1.00	0[1]	U			1				40		
Co. bairdi	19						Nosignificant categories								
L. coccogenis	20	1	−1.50 to 1.50	−0.50 to 0.00	11	R	12	76		20				7	2
O. mykiss	19						No significant categories								
R. cataractae	13						No significant categories								
S. atromaculatus	9	1	−1.50 to 1.00	−1.50 to −0.50	5	R	10	68		6				10	0
		2	−1.00 to 0.50	−1.00 to −0.50	3	R			0	25	18	3			
Autumn 1982															
Availability data	35						26	33	9	14	49	8	4	7	9
		1	−2.50 to 1.50				(0.83)				(0.67)	(0.71)		(−0.66)	(−0.58)
		3	−2.00 to 3.00						(0.87)	(−0.44)					(−0.80)
Cl. funduloides	14						No significant categories								
Co. bairdi	10						No significant categories								
L. coccogenis	10	1	−1.50 to 1.00	−1.50 to −0.50	4	R	4				41	0		13	10
		3	−1.50 to 0.50	−2.00 to −1.00	7	R			0	32					9
O. mykiss	9						No significant categories								

[1]If number of fish is 0 (under-represented), microhabitat use data were taken from microhabitat availablity data for the significant categories.

The majority of water column species exhibited non-random microhabitat use in every season in which they were present at sample sizes greater than six (Table 2). The sole exception to this finding was *N. micropogon*, which failed to display non-random use in both summer 1986 and spring 1988 despite relatively large sample sizes (i.e. 22 and 25 respectively). Water column species generally occupied deeper portions of the study site, however, these species shared few other microhabitat characteristics. Intraspecific analyses indicated that *Cl. funduloides* avoided shallow microhabitats with high amounts of gravel and little bedrock and boulder (Table 2). This species tended to be both over-represented in areas with lower average velocities and under- represented in locations with high average velocities (Table 2). On occasion, however, it also was under-represented in low velocity microhabitats. Responses to other substrata were inconsistent, with a given substratum type being over-represented in some seasons and under-represented in others (Table 2). In general, *Cl. funduloides* exhibited highly variable patterns of microhabitat use.

The remaining water column species displayed a variety of microhabitat use patterns. *Oncorhynchus mykiss* occupied microhabitats with large quantities of cobble and little bedrock. In addition, this species occasionally was over-represented in either deep microhabitats or those with lower average velocities (Table 2). *Luxilus coccogenis* also was over-represented in deeper, lower velocity microhabitats with high amounts of boulder and little gravel (Table 2). *Nocomis micropogon* was over-represented in deep microhabitats with high amounts of debris and little bedrock or gravel. *Semotilus atromaculatus* occupied deep, lower velocity microhabitats with low amounts of erosional substrata and high quantities of depositional substrata (Table 2). Sample sizes for *A. rupestris* only were sufficient for microhabitat analysis in autumn 1989. During this season, *A. rupestris* was over-represented in deep, low-velocity locations, dominated by depositional substrata, with lower than average amounts of cobble and gravel.

Seasonal and hydrologic period differences in microhabitat use

Many seasonal changes in microhabitat use were unambiguously correlated with changes in microhabitat availability (e.g. species occupied deeper microhabitats with higher focal point velocities during seasons in which mean depth and average velocity were significantly greater, Fig. 1, Table 3). For brevity, these results are not extensively described. Significant components from seasonal analyses extracted lower amounts of variance from the microhabitat use data sets than principal component analysis for hydrologic analyses [mean and (range) of variance extracted for benthic species: seasonal=22% (9–52), hydrologic period=40% (15–54), water column species: seasonal=38% (23–56), hydrologic period=43% (3–60)]. This difference was more pronounced for benthic than water column species, and members of the latter guild had more flexible patterns of microhabitat use than benthic guild members.

Benthic guild members

The members of the benthic guild (i.e. *Ca. amomalum, Co. bairdi, E. blennioides, H. nigricans, R. cataractae)* did not display similar patterns of seasonal or hydrologically linked shifts in microhabitat use. Instead, these species appeared to be responding to environmental variation in a species-specific manner.

The two numerically dominant benthic species, *Co. bairdi* and *R. cataractae* both displayed significant seasonal and hydrologic shifts in microhabitat use. The significant seasonal differences exhibited by *Co. bairdi* were attributable to seasonal changes in habitat availability (Fig. 1, Table 3). In hydrologic analyses, however, *Co. bairdi* occupied deeper microhabitats with higher average velocities, greater quantities of erosional substrata and lower amounts of depositional substrata during the pre-drought period than in drought or post-drought samples (Table 4). The seasonal and hydrologic microhabitat shifts displayed by *R. cataractae* probably were produced by the significant differences in mean length displayed by this species in both seasonal and hydrologic analyses (Tables 3-4). This conclusion is warranted because seasonal and hydrologic microhabitat shifts were virtually identical to those elucidated by length-related analyses.

We observed significant seasonal differences in microhabitat use by *Ca. anomalum* that were attributable to seasonal changes in microhabitat availability (Fig. 1, Table 3). In contrast, hydrologic analyses demonstrated that *Ca. anomalum* occupied deeper microhabitats farther from shelter during the post-drought period, than in either pre-drought or drought samples (Table 4). In addition, this species occurred in deeper locations, farther from the substratum and shelter, over more cobble during the drought than in the pre-drought period. Finally, during the drought, *Ca. anomalum* was over-represented in microhabitats with more bedrock and gravel and less cobble and debris than in post-drought samples.

Hypentelium nigricans and *E. blennioides* dis-

Table 3. Seasonal differences in microhabitat use by Coweeta Creek fishes. Seasonal samples with less than 5 individuals were deleted from the analysis. Mean length samples with the same letter are not significantly different. Significant differences were detected using Kruskal-Wallis tests on seasonal PCA scores followed by Tukey-Kramer tests. We only present variables with component loadings ≥|0.40|.

Species	Mean length (cm) Spring (Sp) (*n*)	Summer (S) (*n*)	Autumn (A) (*n*)	Significant component (% variance explained)	Component loadings	Significant differences
Benthic guild						
Ca. anomalum	9.3ª (43)	10.2ª (17)	9.3ª (86)	5 (9)	% bedrock (0.85)	S>A, Sp
Co. bairdi	5.3ª (103)	5.2ª (193)	5.5ª (142)	1 (22)	% cobble (−0.69, % gravel (−0.57), average velocity (−0.79), % sand (0.49), % silt (0.74), % debris (0.65)	S>Sp
E. blennioides		6.8ª (18)	7.2ª (17)	3 (15)	% boulder (−0.48), % silt (−0.42), % cobble (0.55), distance from shelter (0.54), % sand (0.44)	A>S
H. nigricans	11.4ª (5)	15.6ª (19)	15.2ª (19)	4 (12)	% cobble (−0.63), % sand (0.57), % gravel (0.45), distance from shelter (0.43)	Sp, S>A
R. cataractae	4.7ªᵇ (15)	5.4ª (95)	3.8ᵇ (39)	1 (29)	average velocity (−0.79), % cobble (−0.59), % gravel (−0.46), % silt (0.86), distance from substratum (0.74), distance from shelter (0.61), % sand (0.51), % debris (0.45)	A>Sp, S
				2 (13)	% cobble (−0.62), % boulder (0.72), depth (0.51), focal point velocity (0.42)	S>A
				4 (10)	% boulder (−0.48), % bedrock (0.72), % gravel (0.43)	S>A
Water column guild						
Cl. funduloides	5.8ª (150)	5.6ª (244)	5.7ª (192)	1 (21)	% silt (−0.66), % debris (−0.67), focal point velocity (0.76), average velocity (0.83)	S>A
				3 (13)	% bedrock (−0.49), depth (0.61), distance from substratum (0.70), distance from shelter (0.46)	No significant pairs
				4 (11)	% cobble (−0.69), % sand (0.47), distance from shelter (0.60)	No significant pairs
				5 (11)	% bedrock (0.54), % boulder (−0.64)	S>Sp, A
L. coccogenis	7.5ª (47)	7.3ª (44)	8.4ᵇ (87)	1 (19)	average velocity (0.76), distance from substratum (0.50), % sand (−0.48), focal point velocity (0.85)	Sp>A
				2 (17)	% cobble (0.70), % boulder (−0.75), depth (−0.57), % gravel (0.59)	S, SP>A
				5 (10)	% boulder (−0.48), % bedrock (0.61)	A>S
N. micropogon	7.8ª (37)	7.8ª (58)	8.6ª (25)	None significant		
O. mykiss	9.2ªᵇ (44)	7.4ª (94)	11.3ᵇ (86)	1 (23)	% silt (−0.58), % sand (−0.50), % debris (−0.43), depth (0.64), average velocity (0.76), focal point velocity (0.74)	A>Sp, S
S. atromaculatus	10.0ª (7)	9.4ª (79)	11.2ª (13)	2 (16)	% bedrock (−0.64), depth (0.79), distance from substratum (0.57), % cobble (0.54)	SP, A>S
				4 (10)	% sand (−0.78), % boulder (0.64)	S>A

played either seasonal or both seasonal and hydrologic shifts in microhabitat use. In spring and summer, *H. nigricans* occupied locations that were farther from shelter over greater quantities of gravel and sand and lower amounts of cobble than during autumn (Table 3). During the pre-drought period, we found this species at faster focal point velocities, farther from shelter, over more cobble and sand and less bedrock or boulder than during the drought (Table 4). The differences in focal point velocity and distance from shelter may have been influenced by differences in microhabitat availability, because pre-drought samples tended to have higher average velocities than drought samples even though this difference was not statistically significant (Fig. 2). In autumn, we found *E. blennioides* farther from shelter over more rubble and sand and less boulder and silt than during summer (Table 4).

Water column guild members

As with benthic species, there were few similarities in the seasonal and hydrologically-related shifts in microhabitat use exhibited by water column guild members (Tables 3, 4). We detected both seasonal and hydrologic shifts in microhabitat use by *Cl. funduloides*. This species occupied microhabitats with higher average and focal-point velocities and less silt and debris during summer than in autumn (Table 3). In addition, during summer we found *Cl. funduloides* over greater amounts of bedrock and less boulder than in either spring or autumn. With respect to hydrological shifts, many significant differences were attributable to changes in habitat availability. Nonetheless, during the post-drought *Cl. funduloides* occurred in deeper microhabitats farther from the substratum at higher focal-point velocities over more boulder and less

Table 4. Hydrologic period differences in microhabitat use by Coweeta Creek fishes. Hydrologic periods are abbreviated as follows: pre-drought (S83-A84)-PR, drought (S86-S88) - D, post drought (S89-A92) - PO. Seasons with less than 5 individuals were deleted from the analysis. Mean length samples with the same superscript are not significantly different. Significant differences were detected using Kruskal-Wallis tests on PCA scores for hydrologic period data followed by Tukey-Kramer a posterior tests. We only used variables with component loadings ≥|0.40|.

Species	Mean length (cm) PR (*n*)	D (*n*)	PO (*n*)	Significant components (% variance explained)	Component loadings	Significant differences
Benthic guild						
Ca. anomalum	9.2[a] (60)	9.4[a] (51)	9.8[a] (40)	1 (20)	% boulder (−0.61), % cobble (0.45), % sand (0.41), % debris (0.52), depth (0.45), distance from substratum (0.77), distance from shelter (0.46)	D>PR
				3 (15)	% gravel (−0.50), depth (0.47), focal point velocity (0.63), distance from shelter (0.65)	PO>PR, D
				4 (11)	% cobble (−0.41), % gravel (0.63), % sand (0.55), % debris (−0.42)	D>PO
				5 (9)	% bedrock (0.86), % boulder (−0.40)	D>PO
Co. bairdi	5.0[a] (196)	5.2[a] (109)	5.9[b] (133)	1 (22)	average velocity (−0.79), % cobble (0.69), % gravel (−0.57), %silt (0.74), % debris (0.65), % sand (0.49)	PO>PR
				4 (10)	depth (0.54), % bedrock (0.53), distance from substratum (0.48), distance from shelter (0.45)	PR>D, PO
				5 (9)	% bedrock (−0.63), depth (0.53), % boulder (−0.42), distance from substratum (0.41)	PO, PR>D
E. blennioides	7.1[a] (29)	6.8[a] (6)		None significant		
H. nigricans	16.7[a] (7)	14.0[a] (8)	14.8[a] (28)	2 (15)	% boulder (−0.63), % bedrock (−0.46), % cobble (0.58), focal point velocity (0.48), distance from shelter (0.48),% sand (0.45)	PR>D
R. cataractae	5.5[a] (65)	5.5[a] (38)	3.6[b] (46)	1 (29)	average velocity (−0.79), % cobble (−0.59), % gravel (−0.46), % silt (0.86), distance from substratum (0.74), distance from shelter (0.61), % sand (0.50), debris (0.45)	PO>PR, D
				3 (12)	% bedrock (−0.48), focal point velocity (0.61), % sand (0.58)	PO>PR
				4 (10)	% boulder (−0.48), % bedrock (0.72), % gravel (0.43)	PR>PO
Water column guild						
Cl. funduloides	5.9[b] (216)	5.5[a] (149)	5.6[a] (221)	1 (21)	% silt (−0.66), % debris (−0.67), focal point velocity (0.76), average velocity (0.83)	PO>PR
				2 (15)	% boulder (0.69), % cobble (−0.45), % gravel (−0.50), % sand (−0.59), depth (0.46)	PO>PR>D
				3 (13)	% bedrock (−0.49), depth (0.61), distance from substratum (0.70), distance from shelter (0.46)	PO>PR, D
				5 (11)	% bedrock (0.54), % boulder (−0.64)	D, PO>PR
L. coccogenis	8.1[a] (34)	7.2[b] (53)	8.2[a] (91)	1 (19)	% sand (−0.48), distance from substratum (0.50), focal point velocity (0.85), average velocity (0.76)	PO>D, PR
				2 (17)	% boulder (−0.75), depth (−0.57), % cobble (0.70), % gravel (0.59)	D>PR, PO
				4 (12)	% bedrock (−0.51), % silt (0.44), % debris (0.66)	PO>D
N. micropogon		7.3[a] (85)	9.7[b] (35)	1 (18)	% debris (−0.60), % silt (−0.56), average velocity (0.86), focal point velocity (0.56)	PO>D
				3 (12)	% gravel (−0.58), % bedrock (−0.44), % sand (−0.40), depth (0.50), % cobble (0.44), distance from substratum (0.42)	PO>D
O. mykiss	9.7[a] (45)	6.1[b] (54)	10.4[a] (125)	1 (23)	% silt (−0.58), % sand (−0.50), % debris (−0.43), average velocity (0.76), focal point velocity (0.74), depth (0.64)	PO>PR>D
				2 (15)	% gravel (−0.55), % cobble (−0.52), % boulder (0.57), distance from substratum (0.51), % silt (0.41)	PO>PR, D
				3 (12)	% bedrock (−0.55), % gravel (−0.41), % cobble (0.77)	PO>D
S. atromaculatus	8.4[a] (19)	9.0[b] (34)	10.7[c] (46)	2 (16)	% bedrock (−0.64), depth (0.79), distance from substratum (0.57), % cobble (0.54)	PO>PR, D
				3 (12)	% cobble (−0.70), % boulder (0.56), % sand (0.53)	PO>D
				4 (10)	% sand (−0.78), % boulder (0.64)	D>PO

gravel than in either the pre-drought or drought (Table 4, Fig. 1) Focal point velocities may have been affected by the fact that average velocities in the habitat were higher during post-drought than in pre-drought or drought. Finally, this species occupied microhabitats with less bedrock during post-drought and pre-drought than in the drought.

Luxilis coccogenis also exhibited both seasonal and hydrologic shifts in microhabitat use. In spring, this species occurred farther from the substratum, at higher average and focal-point velocities, over lower quantities of sand than in autumn (Table 3). These results probably were influenced by shifts in microhabitat availability, because spring samples tended to have higher average velocities than autumn samples, despite the lack of statistically significant differences in principal component analysis scores for the two seasons (Fig. 1). During spring and summer, we also found *L. coccogenis* in shallower areas with more cobble and gravel and less boulder than in autumn. However, *L. coccogenis* also were significantly larger in autumn than in either summer or spring and larger specimens occupy deeper microhabitats (Tables 3, 5). Finally, in autumn this species occupied locations with more bedrock than in summer. Hydrologic analyses indicated that, during the post-drought period, *L. coccogenis* occurred farther from the substratum, at faster average and focal-point velocities, over less sand than during the pre-drought period (Table 4). Because average velocities were higher during post-drought than pre-drought (and the percentage of sand lower), it is likely that these findings are related to changes in microhabitat availability (Fig. 2). Finally, during the post-drought period we observed this species over more debris and silt and less bedrock than in drought samples.

Like most water column species, *S. atromaculatus* displayed both seasonal and hydrologic shifts in microhabitat use. In spring and autumn, we found *S. atromaculatus* in deeper areas farther from the substratum over less bedrock than in summer (Table 3). Distance from substratum may have been affected by shifts in microhabitat availability, however, because the site was deeper in spring and autumn than in summer (Fig. 1). Nonetheless, during summer this species occupied areas with more boulder and less sand than in autumn. Hydrologic period data indicated that *S. atromaculatus* could be found in deeper microhabitats, farther from the substratum, over more cobble and less bedrock in post-drought than during drought or pre-drought periods (Table 4). Average velocities were faster during post-drought than in pre-drought or drought, which may have affected these results (Fig. 2). *Semotilus atromaculatus* also occupied microhabitats with more sand and cobble in post-drought samples than during the drought (Table 4). Some of these differences may be attributable to length-related variation in microhabitat use because this species was significantly larger in post-drought samples than in either drought or pre-drought samples (Tables 4, 5).

The seasonal or hydrologic shifts in microhabitat use exhibited by both *N. micropogon* and *O. mykiss* were attributable to either changes in microhabitat availability (*N. micropogon*) or significant differences in the mean length of specimens during both seasons and hydrologic periods (*O. mykiss*, Tables 3, 5).

In summary, most significant differences in seasonal microhabitat analyses appeared to be passive responses to shifts in microhabitat availability rather than actual differences in non-random use. The one exception to this generalization involved species for which young-of-the-year constituted a substantial proportion of the total number of individuals measured in seasonal samples (i.e. *O. mykiss*, and *R. cataractae*). The seasonal shifts exhibited by these species appeared to have been produced either by the recruitment of large numbers of small individuals into the population (i.e. *R. cataractae* in autumn) or by length-related shifts in microhabitat use produced as individuals grew in length between spring to autumn (i.e. *O. mykiss*) (Tables 3, 6). The results for hydrologic analyses were similar to those for seasonal analyses (i.e. many significant differences due to changes in microhabitat availability or mean length); however, most species also displayed real shifts in microhabitat use among hydrologic periods. There were few communalities in these responses among species, however, suggesting that the use of spatial resources within this assemblage was based on individualistic responses to changing environmental conditions rather than the reaction of a strongly co-evolved unit. Nonetheless, we did observe several similar responses; for example, *Ca. anomalum*, *Cl. funduloides*, *L. coccogenis* and *S. atromaculatus* all occurred either farther from shelter or the substratum during post-drought than in at least one other hydrologic period. In addition, *Cl. funduloides*, *L. coccogenis* and *S. atromaculatus* all occupied microhabitats with less bedrock during post-drought than in either drought or both pre-drought and drought. Finally both *Ca. anomalum* and *S. atromaculatus* occupied deeper microhabitats in the post-drought than in pre-drought or drought.

Length-related differences in microhabitat use

Length-related analyses of data from pooled samples yielded significant results for three of five benthic species and five of five water column species (Table 5). Length-related differences in microhabitat use generally were restricted to one or two components, and the mean amount of variance extracted for both benthic and water column species was identical (24%), although the ranges differed substantially (benthic species 9–42%, water column species 16–34%). Length-related analyses were affected by the unequal distribution of sizes across seasons and hydrologic periods (Tables 3, 4). Consequently, we did not report results that were clearly attributable to seasonal or hydrologic changes in habitat availability.

Principle component analysis of length-related microhabitat data from individuals observed within a given seasonal sample also extracted one to two significant components for each species (Table 6). The mean amount of variance extracted by these components was slightly higher for benthic species (mean=33%, range 8–48%) than for water column species (mean=25%, range=9–44%), although the ranges were similar (Table 6). When differences existed between analyses based on pooled data and those for individual seasons, we presented results for both analyses.

Of the five benthic species examined, only *E. blennioides*, and *H. nigricans* did not display significant length-based microhabitat shifts (Tables 5, 6). Of the remaining species, pooled data for *Co. bairdi* indicated that large (≥7 cm) and intermediate (5–6 cm) specimens occupied deeper microhabitats, closer to shelter, over more boulder and less bedrock, gravel and sand then small (≤4 cm) members of this species (Table 5). Nonetheless, *Co. bairdi* were significantly larger during post-drought than in either pre-drought or drought, and some of these differences (e.g. substratum) may have been produced by shifts in habitat availability during this period. Data for *Co. bairdi* from individual seasonal samples indicated that during summer 1986, larger specimens (≥6 cm) occupied deeper microhabitats farther from shelter, with lower average and focal-point velocities, over greater amounts of depositional substrata and lower quantities of erosional substrata than smaller (≤5 cm) *Co. bairdi* (Table 6). Similarly, in summer 1988, larger (≥6 cm) *Co. bairdi* were found in deeper areas with lower average and focal-point velocities over more debris and silt and less gravel than smaller (≤5 cm) *Co. bairdi* (Table 6). In autumn 1989, larger (≥6 cm) *Co. bairdi* occupied locations closer to shelter, with higher average velocities and greater quantities of cobble and gravel, and lower quantities of depositional substrata, than smaller (≤4 cm) specimens of this species. Similarly, in summer 1992, larger (≥6 cm) sculpins occupied locations with higher average and focal-point velocities, more cobble and gravel, and less sand, silt, and debris than small (≤5 cm) *Co. bairdi*. Length-related shifts in microhabitat use by *C. bairdi* appeared to be strongly affected by hydrologic period (i.e. compare drought data with post-drought data).

Both *R. cataractae* and *Ca. anomalum* displayed significant length-related shifts in microhabitat use. Analyses of pooled data indicated that large (≥7 cm) *R. cataractae* occupied microhabitats that were closer to both shelter and the substratum, with higher average velocities, over greater amounts of erosional substrata and lower quantities of depositional substrata, than either intermediate (5–6 cm) or small (≤4 cm) specimens (Table 5). The same relationship was present between intermediate and small (≤4 cm) *R. cataractae*. In addition, intermediate (5–6 cm) *R. cataractae* occupied deeper microhabitats with higher focal point velocities, greater quantities of boulder and less cobble than either large or small members of this species. Seasonal analyses yielded similar results when significant differences were detected (Table 6). In analyses of pooled data, large (≥10 cm) *Ca. anomalum* were found over less bedrock than intermediate (8–10 cm) and small (≤7 cm) *Ca. anomalum*. Seasonal data displayed a somewhat different pattern, however, and in autumn 1986 small (≤9 cm) *Ca. anomalum* occupied shallower microhabitats closer to shelter, with higher average velocities, over more cobble and less sand gravel and boulder than large (≥10 cm) specimens (Table 6). In addition, during autumn 1989, we found large (≥9 cm) members of this species over more debris and less bedrock than small (≤8 cm) *Ca. anomalum*.

All members of the water-column guild, with the exception of *A. rupestris* (insufficient numbers), exhibited length-related changes in microhabitat use. Pooled analysis indicated that large (≥7 cm) *Cl. funduloides* occurred closer to shelter, at higher average and focal-point velocities, over more cobble and lower quantities of depositional substrata than intermediate (5–6 cm) and small (≤4 cm) *Cl. funduloides* (Table 5). Seasonal analyses displayed a greater level of variation in length-based microhabitat shifts for *Cl. funduloides* (Table 6). During spring 1988, we found large (≥7 cm) *Cl. funduloides* closer to both shelter and the substratum, at lower focal-point velocities over more cobble and gravel and less bedrock than smaller (≤5 cm) members of this species (Table 6). In summer 1989, large and intermediate-sized (≥6 cm) individuals occurred closer to shelter over more cobble, sand and debris and less boulder than small (≤4 cm) *Cl. funduloides*. Similarly, in summer 1990 large (≥7 cm) *Cl. funduloides* were found closer to the substratum at higher average and focal point velocities over more bedrock and less cobble, sand and silt than small and intermediate-sized specimens (≤6 cm). Finally, in autumn 1990, large (≥7 cm) *Cl. funduloides* occupied deeper microhabitats farther from shelter, at lower focal-point velocities, over less boulder than small (≤4 cm) and intermediate-

Table 5. Results of principal componant analysis on length-related shifts in microhabitat use (pooled data). Data were tested using Mann-Whitney (2 size groups) or Kurskal-Wallis tests (≥3 size groups) with Turkey-Kramer a posterior tests. We only present variables with loadings ≥|0.40|.

Species	Size classes	*n*	Significant component (% variance explained)	Component loadings	Significant differences
Benthic guild					
Ca. anomalum	≤7	22	5 (9)	% bedrock (0.91)	(≤7) (8–10)>(>10)
	8–10	90			
	>10	48			
Co. bairdi	≤4	115	3 (11)	% sand (0.57), distance from shelter (0.53), % gravel (0.40), % boulder (−0.43)	(5–6) (≥7)<(≤4)
	5–6	234			
	≥7	89			
			5 (9)	depth (0.53), % boulder (0.42), distance from substratum (0.41), % bedrock (−0.63)	(≥7) (5–6)>(≤4)
E. blennioides	<6	19	None significant		
	7–8	17			
	>8	9			
H. nigricans	≤11	12	None significant		
	12–15	24			
	16–18	13			
	≥19	14			
R. cataractae	≤4	68	1 (29)	% silt (0.86), distance from substratum (0.74), distance from shelter (0.62), % sand (0.48), % debris (0.46), average velocity (−0.79), % cobble (−0.59), % gravel (−0.46)	(≥7)<(5–6)<(≤4)
	5–6	56			
	≥7	34			
			2 (13)	% boulder (0.67), depth (0.51), focal point velocity (0.49), % cobble (−0.59)	(5–6)>(≤4)(≥7)
Water column guild					
Cl. funduloides	<4	66	1 (21)	average velocity (0.83), focal point velocity (0.76), % debris (−0.67), % silt (−0.66)	(≥7)>(5–6)(≤4)
	5–6	389			
	≥7	131			
			4 (11)	distance from shelter (0.60), % sand (0.47), % cobble (−0.69)	(≥7)<(≤4)(5–6)
L. coccogenis	≤6	38	2 (17)	% boulder (0.77), depth (0.62), % cobble (−0.65), % gravel (−0.61)	(7–9)>(≤6)
	7–9	107			
	≥10	37			
N. micropogen	≤6	32	3 (12)	% cobble (0.50), depth (0.45), % gravel (−0.61), % sand (−0.50), % bedrock (−0.44)	(7–9)(≥10)>(≤6)
	7–9	66			
	≥10	26			
			4 (11)	average velocity (0.83), focal point velocity (0.56), % silt (−0.56), % debris (−0.60)	(≥10)>(≤6)
O. mykiss	≤5	50	1 (23)	average velocity (0.76), focal point velocity (0.75), % depth (0.63), distance from shelter (0.43), % silt (−0.59), % sand (−0.47), % debris (−0.46)	(6–8) (9–12) (≥13)>(≤5) (≥13)>(6–8)
	6–8	87			
	9–12	34			
	≥13	59			
			4 (11)	% sand (0.55), distance from substratum (0.54), % bedrock (−0.50)	(≥13)>(6–8)
S. atromaculatus	≤8	50	2 (16)	depth (0.76), % cobble (0.56), distance from substratum (0.56), % bedrock (−0.65)	(≥15) (13–14) (9–12)>(≤8)
	9–12	33			
	13–14	13			
	≥15	9			

sized specimens (≤6 cm). Analyses from individual seasonal samples revealed that larger *Cl. funduloides* tended to occur closer to both the substratum and shelter over increasing amounts of cobble and gravel and less boulder, although seasonal analysis did not exhibit the consistent positive relationship between size and velocity observed in pooled analysis.

Analyses of pooled data for *Luxilus coccogenis* indicated that intermediate (7–9 cm) *L. coccogenis* occurred in deeper locations with greater amounts of boulder and less cobble and gravel than small (≤6 cm) members of this species (Table 5). Although the depth effect may have been influenced by the fact that larger *L. coccogenis* were more common during hydrologic periods in which the site was deeper (Table 4), we observed both concordant and dissimilar results in seasonal length-related analyses (compare summer 1992 and autumn 1989). In fact, this species displayed highly variable patterns of length-related microhabitat use in seasonal samples (Table 6). In autumn 1986, larger (≥9 cm) *L. coccogenis* occurred farther from both the substratum and shelter, at faster average and focal-point velocities, over less debris than smaller *L. coccogenis* (Table 6). During autumn

Table 6. Results of principal component analysis on length-related shifts in microhabitat use (individual seasons). Seasons are abbreviated as follows: Sp=spring, S=summer, A=autumn, significant differences were elucidated using Mann-Whitney (2 size groups) or Kruskal-Wallis with Tukey-Kramer tests (≥3 size groups) on principal component analysis scores. Non-significant results are not reported. We only present variables with component loadings ≥|0.40|.

Species	Season	Size class (cm) (*n*)	Significant component	Component loadings	Significant differences
Benthic guild					
Ca. anomalum	A86	≤9, ≥10 (10) (7)	1 (32)	average velocity (−0.73), % cobble (−0.71), % sand (0.83), % gravel (0.78), depth (0.77), distance from shelter (0.57), % boulder (0.49)	(≥10)>(≤9)
	A89	≤8, ≥9 (8) (14)	5 (8)	% debris (−0.44), % bedrock (0.84)	(≤8)>(≥9)
Co. bairdi	S86	≤5, ≥6 (18) (14)	1 (31)	average velocity (−0.84), % cobble (−0.68), % gravel (−0.53), % silt (0.88), % debris (0.73), distance from shelter (0.47), depth (0.48)	(≥6)>(≤5)
			2 (17)	% sand (−0.68), focal point velocity (0.63), distance from shelter (0.52), % boulder (0.48), % gravel (0.47)	(≥6)≤(≤5)
	S88	≤5, ≥6 (15) (11)	1 (28)	% debris (−0.60), % silt (−0.58), depth (−0.51), average velocity (0.88), focal point velocity (0.84), % gravel (0.73)	(≥6)<(≤5)
	A89	≤5, ≥6 (13) (9)	1 (37)	average velocity (−0.92), % cobble (−0.72), % gravel (−0.51), % sand (0.86), % silt (0.86), distance from shelter (0.61), % debris (0.40)	(≤6)<(≥5)
	S92	≤5, ≥6 (9) (10)	1 (44)	% silt (−0.88), % debris (−0.83), % sand (−0.79), % cobble (0.93), % gravel (0.86), average velocity (0.60), focal point velocity (0.54)	(≥6)>(≤5)
R. cataractae	S88	≤4, 5–6, ≥7 (5) (8) (6)	1 (34)	average velocity (−0.59), % cobble (−0.54), % sand (0.88), distance from substratum (0.87), distance from shelter (0.85), % silt (0.76), % debris (0.45), depth (0.44)	(≥7)<(≤4)
Water column guild					
Cl. funduloides	Sp88	≤5, 6, ≥7 (25) (8) (12)	2 (22)	% cobble (−0.60), % gravel (−0.49), distance from shelter (0.73), % bedrock (0.63), depth (0.56), focal point velocity (0.55), distance from substratum (0.54)	(≥7)<(≤5)
	S89	≤4, 5, ≥6 (8) (23) (4)	2 (19)	% boulder (−0.79), distance from shelter (−0.58), % cobble (0.70), % sand (0.43), % debris (0.42)	(≥6)>(≤4)
	S90	≤6, ≥7 (21) (9)	1 (26)	% bedrock (−0.65), focal point velocity (−0.63), average velocity (−0.40), distance from substratum (0.78), % sand (0.77), % silt (0.63), % cobble (0.44)	(≥7)<(≤6)
L. coccogenis	A86	≤8, ≥9 (6) (7)	1 (29)	% debris (−0.89), distance from shelter (0.77), focal point velocity (0.77), average velocity (0.72), distance from substratum (0.52)	(≥9)>(≤8)
	A89	≤7, ≥8 (7) (14)	2 (17)	% boulder (−0.75), depth (−0.53), % cobble (0.57), distance from shelter (0.44), focal point velocity (0.40)	(≥8)<(≤7)
			3 (14)	% debris (−0.72), % gravel (0.76)	(≥8)<(≤7)
	Sp90	≤8, ≥9 (7) (8)	2 (22)	% gravel (−0.77), % sand (−0.44), distance from shelter (0.85), distance from substratum (0.69), % silt (0.44)	(≥9)<(≤8)
N. micropogon	Sp88	≤7, ≥8 (16) (9)	4 (13)	% cobble (−0.77), % bedrock (0.69), distance from substratum (0.51)	(≥8)>(≤7)
	S88	≤7, 8–9, ≥10 (8) (10) (7)	2 (19)	% bedrock (−0.59), distance from substratum (0.71), depth (0.70), % debris (0.53), % sand (0.46)	(8–9)(≥10)>(≤7)
	S89	≤8, ≥9 (6) (5)	3 (16)	depth (−0.49), % sand (0.83), distance from substratum (0.74)	(≥9)>(≤8)
O. mykiss	Sp88	≤3, ≥4 (7) (13)	5 (9)	% boulder (−0.49), % gravel (−0.40), % cobble (0.47), distance from shelter (0.44), % sand (0.41)	(≥4)>(≤3)
	S88	≤6, ≥7 (16) (5)	3 (15)	% bedrock (−0.73), distance from substratum (−0.41), distance from shelter (0.63), % sand (0.50)	(≥7)>(≤6)
	S89	≤5, ≥6 (7) (14)	1 (25)	% boulder (−0.60), distance from substratum (−0.52), % silt (−0.52), % sand (−0.45), distance from shelter (−0.42), % cobble (0.81), average velocity (0.72), focal point velocity (0.53), % gravel (0.42)	(≥6)<(≤5)
	A90	≤10, ≥11 (9) (13)	1 (27)	% debris (−0.72), % silt (−0.69), % cobble (−0.69), % boulder (0.66), depth (0.60), average velocity (0.52), focal point velocity (0.49), distance from shelter (0.49)	(≥11)>(≤10)
	S92	≤8, ≥9 (14) (5)	1 (29)	% cobble (−0.89), % debris (−0.62), % gravel (0.65), distance from substratum (0.62), depth (0.61), % boulder (0.50), % sand (0.43)	(≥9)>(≤8)
			3 (15)	% sand (−0.74), distance from shelter (−0.48), % boulder (0.64), depth (0.42)	(≥9)<(≤8)
S. atromaculatus	S88	≤8, ≥9 (9) (13)	1 (41)	average velocity (−0.85), focal point velocity (−0.73), % bedrock (−0.64), % sand (−0.46), % gravel (−0.42), depth (0.79), % debris (0.77), distance from substratum (0.74), % silt (0.73), % boulder (0.56)	(≥9)>(≤8)
	S90	≤9, ≥10 (5) (6)	2 (23)	distance from shelter (−0.74), % sand (−0.69), average velocity (−0.46), distance from substratum (0.74), % boulder (0.69), depth (0.46)	(≤9)>(≥10)

1989, however, we found smaller (≤7 cm) *L. coccogenis* in shallower microhabitats farther from shelter, at faster focal-point velocities over less boulder than larger (≥8 cm) members of this species. Smaller *L. coccogenis* also occurred over more gravel and less debris than larger *L. coccogenis*. Finally in spring 1990, smaller (≤8 cm) *L. coccogenis* also occupied microhabitats farther from shelter and the substratum over more silt and less gravel and sand than *L. coccogenis* 9 cm in length or greater. Like several other species, larger *L. coccogenis* exhibited one set of responses during drought (i.e. higher focal-point velocity and farther from shelter) and a different set during post-drought (i.e. lower focal-point velocity and closer to shelter).

Pooled length-related data for *N. micropogon* showed that large (≥10 cm) and intermediate (7–9 cm) specimens occupied deeper microhabitats, with more cobble and less gravel, sand, and bedrock, than small (≤6 cm) *N. micropogon* (Table 5). Although larger *N. micropogon* were more abundant during the deeper post-drought period, larger specimens also occupied significantly deeper locations during the drought (summer 1988, Table 6). This species also exhibited significant length-related differences in microhabitat use in three of six seasons (Table 6). In spring 1988 larger (≥8 cm) *N. micropogon* occurred farther from the substratum over more bedrock and less cobble than smaller (≤7 cm) members of this species. During summer 1988 larger (≥8 cm) *N. micropogon* also occupied deeper microhabitats farther from the substratum, over more debris and sand, and less bedrock than smaller (≤7 cm) *N. micropogon* (Table 6). Finally, in summer 1989, we found larger (≥9 cm) *N. micropogon* in shallow microhabitats, farther from the substratum over more sand than smaller (≤8 cm) *N. micropogon*. It is unclear why pooled data did not display the significant differences in distance from substratum between large and small *N. micropogon* observed in the three significant seasonal analyses. In general, seasonal analyses demonstrated that larger *N. micropogon* occurred farther from the substratum than smaller members of this species; a distinct result from those obtained through pooled analyses. Finally, *N. micropogon* displayed different length-related shifts in microhabitat use between drought and post-drought samples. During the former period larger *N. micropogon* occupied deeper microhabitats whereas in post-drought larger members of this species were found in shallower microhabitats (Table 6).

Analyses of pooled data for *O. mykiss* indicated that large and intermediate-sized members of this species occurred in deeper locations, at higher average and focal point velocities, farther from the substratum and shelter, over lower amounts of depositional substrata, than small (≤5 cm) *O. mykiss* (Table 5). Identical results were obtained between large (≥13 cm) individuals of this species (deeper, faster, etc.) and intermediate (6–8 cm) *O. mykiss*. Seasonal data showed that *O. mykiss* (≥7 cm) tended to occur farther from both shelter and the substratum and over more boulder substrata and less cobble and gravel than smaller (≤6 cm) *O. mykiss* (Table 6). Larger members of this species also occasionally occupied deeper microhabitats than smaller *O. mykiss* (autumn 1990 and summer 1992) although in summer 1992 some small (≤8 cm) *O. mykiss* also occurred in deeper microhabitats than larger (≥9 cm) specimens (component 3, Table 6). Pooled and seasonal analyses yielded similar results with the exception of velocity and depth data.

Pooled analyses for *S. atromaculatus* indicated that larger specimens (i.e. ≥9 cm) occupied deeper locations, farther from the substratum, with more cobble and less bedrock than small (≤8 cm) *S. atromaculatus* (Table 5). Seasonal analysis displayed little consistency among length-related microhabitat shifts (Table 6). In summer 1988, we found larger (≥9 cm) *S. atromaculatus* in deeper microhabitats with lower average and focal point velocities, more boulder, silt and debris, and less bedrock, gravel and sand than smaller (≤8 cm) members of this species (Table 6). Conversely, in summer 1990, smaller (≤9 cm) *S. atromaculatus* occupied deeper locations, with lower average velocities, farther from the substratum, closer to shelter, over more boulder and less sand than larger (≥10 cm) *S. atromaculatus* (Table 6). The lack of concordance between pooled and seasonal analyses is probably due to several sources including: 1) responses to differing hydrologic conditions among hydrological periods, 2) differences in sample size, and 3) differences in length classes (Table 4).

There were several general patterns present in either pooled or seasonal length-related microhabitat analyses. Among benthic species, larger *R. cataractae* occurred closer to shelter, at higher average and focal-point velocities than smaller *R. cataractae;* a pattern that also was recorded for *Co. bairdi* during the post-drought period (but not drought). As with *R. cataractae*, larger *Ca. anomalum* also occupied microhabitats with faster focal point velocities than smaller members of this species. Within the water-column guild, larger specimens tended to occupy deeper microhabitats (*L. coccogenis, N. micropogon, O. mykiss*, and *S. atromaculatus*), farther from the substratum (*L. coccogenis, O. mykiss*, and *S. atromaculatus*), over lower quantities of depositional substrata (*Cl. funduloides, N. micropogon,* and *O. mykiss*) than smaller specimens. It is worth noting, however, that these responses were not always observed in both pooled and seasonal analyses for a given species (Tables 5, 6). In fact, the patterns of length-related microhabitat use exhibited by individual species (e.g. *Ca. anomalum, Co. bairdi, L. coccogenis, O. mykiss, S. atromaculatus*) frequently differed among hydrologic periods even when differential microhabitat availability was accounted for.

Discussion

The members of the Coweeta Creek fish assemblage exhibited non-random microhabitat use (sensu Grossman & Freeman 1987) in a majority of samples, as well as substantial seasonal, hydrologic, and length-related shifts in the utilization of spatial resources. These results suggest that the microhabitat requirements of assemblage members are relatively flexible. Our quantification of this flexibility should aid in the design and implementation of future management plans or tests of theory involving members of the Coweeta Creek fish assemblage.

Despite their rather general microhabitat use patterns, most species displayed non-random microhabitat use in all samples, with the exception of two benthic (*Co. bairdi* and *H. nigricans*) and one water column species (*N. micropogon*) species. Even these fishes generally exhibited selection with respect to distance from the substratum (i.e. *Co. bairdi* always occurred on the substratum, whereas *N. micropogon* always occupied the water column) although it was difficult to test distance from the substratum measurements against a comparable aspect of microhabitat availability (e.g. the random position of an object in the water column) without rendering the comparison trivial. We did observe several general trends in microhabitat use among assemblage members, the most prominent being the over-representation of most benthic and water column guild members in the deeper portions of the site (Table 2). Within the benthic guild, all species except *C. bairdi* and small *R. cataractae* also were over-represented in locations with greater than average amounts of erosional substrata. Water column guild members generally were over-represented in locations with lower average velocities, with the exceptions being *N. micropogon* and *O. mykiss* (four of six seasons). In addition, water column species exhibited highly variable patterns of substratum use.

Although most species shifted microhabitat use in response to seasonal and hydrologic variations in microhabitat availability, analyses based on the relationship of a given sample to the drought (i.e. hydrologic period) produced greater statistical separation of samples in both microhabitat availability and fish microhabitat use data sets. These results indicate that the effects of the drought, and subsequent high-water years, on the physical characteristics of the site were substantially stronger than those experienced through seasonal variation both within and among years. This is not unexpected, given that the study period included some of the lowest and highest mean daily flows recorded in the last 55 years (Grossman et al. 1995a). In contrast, the responses of most fishes to seasonal variations in microhabitat availability appeared to be passive (i.e. shifts to deeper microhabitats when average depth of the site increased), whereas differences in microhabitat use among hydrologic periods contained a higher proportion of responses that were not strongly correlated with changes in microhabitat availability. There were some communalities among species in these responses, although they only involved a maximum of three out of a total of ten possible species [e.g. *L. coccogenis, S. atromaculatus,* and *Ca. anomalum*, occupied positions farther from either the substratum or shelter (these parameters were correlated for most species), during the post-drought than in either the pre-drought or drought]. However, given that a majority of species exhibited distinct hydrologic shifts in microhabitat use, it appears that assemblage members are responding to changes in microhabitat availability in a species-specific manner, rather than as part of a strongly interacting guild. Finally, our results also demonstrate the need for quantifying resource use patterns of fishes over time scales which encompass the range of environmental variations likely to be experienced by these species during planned management activities (e.g. 10 years, 20 years, etc.). This may be particularly important for species with small populations, given that unpredictable disturbances such as floods and droughts may cause substantial mortality in stream fishes (Seegrist & Gard 1972; Schlosser 1985; Erman et al. 1988; Harvey 1987).

We elucidated length-related differences in microhabitat use using two different data sets: 1) all specimens pooled across all samples and 2) separate data sets for each seasonal sample). We conducted analyses on two data sets because: 1) within pooled data sets, there was an unequal distribution of length classes across seasons and hydrologic periods, coupled with significant differences in microhabitat availability among these periods, and 2) within individual seasonal samples, the numerical abundances of length classes frequently appeared to be insufficient to characterize the length-related differences in microhabitat use manifested by most species. Despite the shortcomings of each data set, we obtained similar results from both analyses for three water column and one benthic species. Nonetheless, the remaining four species (two benthic and two water column) exhibited a lack of concordance between data from pooled and individual seasonal analyses. It is possible that most of these discrepancies are related to differences in: 1) microhabitat availability, 2) the distribution of length classes, or 3) sample sizes, between these two data sets. In addition, analyses based on individual seasons indicated that four species (*Co. bairdi, L. coccogenis, N. micropogon,* and *S. atromaculatus*) displayed distinct patterns of length-related shifts in microhabitat use in different hydrologic periods (e.g. *L. coccogenis* - larger specimens were found farther from shelter and the substratum during the drought whereas the opposite response was observed in the post-drought). These findings demonstrate that variations in microhabitat availability have a strong effect on the length-related shifts in microhabitat use exhibited by Coweeta fishes, and also re-emphasize the need for accurate quantification of microhabitat use patterns of fish if resource-based management models are to have predictive value.

Length-related microhabitat analyses did yield similar results for several species. For example, larger individuals of two benthic species (*Ca. anomalum* and *R. cataractae)* both occupied locations with faster average velocities than those utilized by smaller individuals. This pattern also was exhibited by *Co. bairdi* during the post-drought, however the opposite result was observed during the drought (i.e. larger specimens found at lower average velocities). Finally, four of five water column species exhibited a pattern where larger specimens occurred in deeper microhabitats than smaller members of these species.

Some of our findings are similar to those reported by other researchers who have studied microhabitat use in stream fishes. For example, stream fishes frequently exhibit substantial variability in their use of spatial resources (Angermeier 1987, McNeeley 1987, Ross et al. 1987, Bart 1989, Freeman & Grossman 1987, Brown & Moyle 1991, Grossman & De Sostoa 1994a, b, Brown et al. 1995, Wood & Bain 1995). In fact, several researchers were unable to correctly classify a majority of specimens to species based on discriminant function analyses of microhabitat use data (McNeeley 1987, Ross et al. 1987), a result obtained for both benthic and water column fishes. In addition, it is not uncommon for stream fishes to exhibit seasonal shifts in microhabitat use that appear to be passive responses to changes in microhabitat availability, rather than shifts in microhabitat selection (Baltz & Moyle 1984, Grossman & Freeman 1987, Heggenes & Saltveit 1990, Rincon & Lobón-Cervía 1993). Nonetheless, other investigators have observed significant seasonal shifts in microhabitat use that were not correlated with changes in microhabitat availability (Baltz et al. 1991). One unusual finding of our study was that annual variations in flow (i.e. drought *vs* high flows) elicited much stronger microhabitat shifts by assemblage members than seasonal changes in microhabitat availability. Although we are unaware of other studies that support this result, it should be noted that multi-year studies of microhabitat use in stream fishes are uncommon.

It is not unusual for stream fishes to be overrepresented in the deeper portions of streams (Angermeier & Karr 1984, Power 1984, Grossman & De Sostoa 1994a, b), and this result has been interpreted as an avoidance response of avian and terrestrial predators (Power 1984, Harvey & Stewart 1991). A similar explanation has been proposed for the observation that larger individuals of a given species also frequently occupy deeper locations than smaller specimens (Anderson 1985, Schlosser 1987, Harvey & Stewart 1991), a finding also observed among most water column guild members at Coweeta. We have examined the effects of potential predators on microhabitat use by assemblage members and found little evidence that piscine predators [i.e. *A. rupestris* (≥15 cm), *S. atromaculatus* (≥15 cm) and *O. mykiss* (≥20 cm)] produced microhabitat shifts in these species (Grossman & Freeman 1987, Grossman et al. 1995b, in press). In addition, avian and terrestrial predators are uncommon in this system (Grossman & Freeman 1987, Grossman et al. personal observation). Hence, it is unlikely that predators have produced the depth-distribution patterns observed in this assemblage. Harvey & Stewart (1991) also have suggested that predator-mediated shifts to deeper microhabitats are less common in high velocity systems like Coweeta Creek, than they are in streams with lower mean velocities.

If predation has little effect on microhabitat use by assemblage members, perhaps fishes are choosing microhabitats on the basis of maximization of their net energy gain (Hill & Grossman 1993). This process could have produced the results we obtained because these optima probably differ both among species and among size classes within a species (Hill & Grossman 1993). In fact, Hill & Grossman (1993) demonstrated that larger *Cl. funduloides* and *O. mykiss* maximized their net energy gain by occupying faster focal-point velocities in Coweeta Creek than those utilized by smaller individuals. Faster focal-point velocities yielded greater rates of energy gain for larger specimens, because there was a positive relationship between prey availability and velocity, and larger fishes were better able to maintain position and capture prey at higher velocities than smaller individuals. Our pooled data confirmed this fish length – focal-point velocity relationship for both species; however, principal component analysis from individual seasonal samples indicated that larger *Cl. funduloides* did not always occupy faster focal-point velocities than smaller *Cl. funduloides*. We obtained a similar result for *O. mykiss*. There are several possible explanations for these discrepancies. First, our sample sizes were much smaller than those of Hill & Grossman (1993). Second, our analyses also included size classes beyond the range studied by Hill & Grossman (1993). Third, Hill & Grossman (1993) conducted their study during the drought, and the current study showed that both of these species shifted their patterns of length-related microhabitat use after the drought. Finally, when we examined mean focal point velocities (rather than the principal component analysis) using size classes similar to those of Hill & Grossman (1993), we found that larger specimens did occupy faster focal point velocities during seven of eight seasons in which comparisons could be made (*Cl. funduloides* – five seasons, *O. mykiss* – three seasons). Nonetheless, this difference frequently was small (i.e. 1–2 cm/s) and could not be tested statistically due to small sample sizes.

Energy maximization mechanisms also may play a role in microhabitat use by benthic species in Coweeta Creek. Facey & Grossman (1992) have shown that energetic constraints apparently do not affect microhabitat use by *Co. bairdi* in Coweeta Creek, and Petty & Grossman (1996) demonstrated that prey abundance was a better predictor of patch choice by this species in the Coweeta drainage than physical factors alone. Given the lack of energetic constraints on microhabitat use by *Co. bairdi*, Petty & Grossman (1996) suggested that the strong correlation between high prey abundance and occupancy of a given patch by this species also represented an energy maximization strategy.

It is also possible that some of the length-related variation observed among Coweeta fishes is a consequence of intraspecific competition. Freeman & Stouder (1989) demonstrated that this process influenced the depth distribution of *Co. bairdi* in Coweeta Creek during the drought (i.e., larger specimens deeper). Although the size classes used in the two studies differed slightly, our data suggest that depth selection by large and small *Co. bairdi* may be strongly affected by hydrologic period (i.e. microhabitat availability). Although our pooled analyses indicated that larger *Co. bairdi* occupied deeper microhabitats than smaller members of this species, individual seasonal analyses only detected this result in two of eleven possible seasons (includes seasons with nonsignificant results), both of which occurred during the drought. Consequently, if intraspecific competition affected the differential depth distributions of large and small sculpins, it may have been most important in seasons when microhabitat availability was highly constrained (i.e. summer 1986 and 1988). Little is known about intraspecific competitive relationships within the remaining species, hence, the effect of this process on microhabitat shifts by these species is unknown. In addition, concurrent studies also suggest that interspecific competition had little effect on microhabitat use by assemblage members (Barrett 1989, Stouder 1990, Grossman & Boule 1991, Freeman & Grossman 1992, Grossman et al. in press, Rincon & Grossman 1997). In conclusion, we suspect that the patterns of non-random microhabitat use observed within this assemblage are a result of differential species-specific responses to changing environmental conditions, rather than interspecific interactions such as predation or interspecific competition.

Our data, although long term, come from a single site on one stream. Given that some species exhibit distinct patterns of microhabitat use in different systems (Angermeier 1987, Wood & Bain 1995), it is worthwhile to compare our results to those of other investigators working in different systems. Although few of these researchers employed under-water observational techniques, their findings possess both similarities and differences when compared to our results. For example, many investigators have found that *R. cataractae* exhibit length-related shifts in microhabitat use with larger specimens occupying high velocity areas with erosional substrata, whereas smaller individual are found in low-velocity microhabitats (Gee & Northcote 1963, Gibbons & Gee 1972, Kelsch 1994, Mullen & Burton 1995), a pattern also observed in Coweeta Creek. In addition, Culp (1989) demonstrated that in Alberta prairie streams, *R. cataractae* frequently is found under cobbles during the day, and is active only during the night. In Coweeta Creek, however, we have regularly observed active *R. cataractae* during daylight hours (G. Grossman & A. Thompson, unpublished data), and a diel feeding study of this species indicated that *R. cataractae* foraged throughout the day (A. Thompson, G. Grossman, and S. Floyd, unpublished data). Coweeta Creek is a very different habitat (i.e. a forested mountain stream) from the Canadian prairie streams studied by Culp

(1989), and this probably contributes to our disparate results.

With respect to the remaining species, several authors have shown that *S. atromaculatus* is overrepresented in deep, low velocity locations (Minckley 1963, Moshenko & Gee 1973, Hubert & Rahel 1989) although there appears to be geographic variation in this response (see Angermeier 1987). Our findings for *O. mykiss* also appear to be similar to those observed by Baltz & Moyle (1984), Moyle and Baltz (1985) and Baltz et al. (1991). In addition, Angermeier (1987) recorded *Ca. anomalum* from low-velocity habitats which sometimes were of greater than average depth, a result which is in partial agreement (i.e. deeper) with our observations from Coweeta Creek. Finally, both Fahy (1954) and Winn (1958) found *E. blennioides* in high-velocity riffles with cobble substrata, whereas in our study this species occupied deeper locations with boulder substrata.

In conclusion, our results demonstrate that members of the Coweeta fish assemblage consistently occupied a subset of the available habitat, and that microhabitat use by these species was strongly affected by environmental variation in the form of droughts and floods. In addition, many species exhibited strong length-related shifts in microhabitat use, some of which varied substantially with changes in water levels (i.e. hydrologic period). These findings demonstrate that Coweeta fishes have very flexible microhabitat requirements, and also indicate that inferences about assemblage members should be limited to the range of environmental conditions under which a given set of results are obtained. If similar patterns exist within other stream fish assemblages, it is likely that considerable data will have to be gathered before resource-based management models can be effectively used to manage these assemblages or predict their responses to environmental change.

Resumen

1. Hemos registrado el uso del microhabitat por parte de los miembros de una comunidad de peces fluviales del sur de los Apalaches (USA) a lo largo de diez años, período que incluye tanto sequías como crecidas. La localidad de estudio (de 37 m de longitud) comprendió pozas, tablas y chorreras.
2. Investigaciones preliminares indicaron que las especies se distribuían en dos grupos: especies bentónicas y de columna de agua. La mayoria de las especies mostraron un uso no-aleatorio del microhábitat en todas las estaciones del año y las especies de ambos grupos fueron más comunes de lo que cabía esperar en las zonas más profundas de la localidad. Además, las especies de la columna de agua fueron más numerosas de lo esperado en las zonas de baja velocidad media del agua.
3. La mayoría de los cambios estacionales en el uso de microhábitat fueron pasivos (es decir, relacionados con cambios en la disponibilidad de los microhábitats), mientras que las variaciones observadas en distintos períodos hidrológicos (sequías y crecidas) parecieron ser respuestas activas a las condiciones ambientales cambiantes.
4. La mayoría de las especies mostraron diferencias en el uso del microhabitat entre ejemplares de diferentes tamaños y éstas estuvieron fuertemente influenciadas por el período hidrólogico en cuatro de diez especies.
5. Los patrones de uso del microhábitat de los miembros de esta comunidad mostraron ser consecuencia de respuestas propias de cada especie a las condiciones ambientales cambiantes. Dado que dichos patrones son bastante flexibles, las decisiones relativas a la gestión de estas especies debería basarse en datos que cubran una amplia variedad de circunstancias ambientales.

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